Deadwood, soil biota and nutrient dynamics in tropical forests: a review of studies from Puerto Rico

Grizelle González

*Project Leader, USDA Forest Service – International Institute of Tropical Forestry
Jardín Botánico Sur, 1201 Calle Ceiba, San Juan, PR
ggonzalez@fs.fed.us

Deadwood

Important structural component of forests (CWD)

Forest	% of the abovegr. litter	Mg/ha
Tropical	20-30	10-55
Temperate	up to 70	10-200

Deadwood

Habitat for fungi, insects, birds, frogs and small mammals

Seed germination and seedling establishment

Deadwood

Source of nutrients:

- Leaching
- Fungi fruiting bodies
- Turnover of decomposers biomass
- Animals

C and nutrients sink:

- Low decomposition rate
- Immobilization of nutrients in decomposers biomass

Nitrogen fixation

Water storage

Soil formation and development

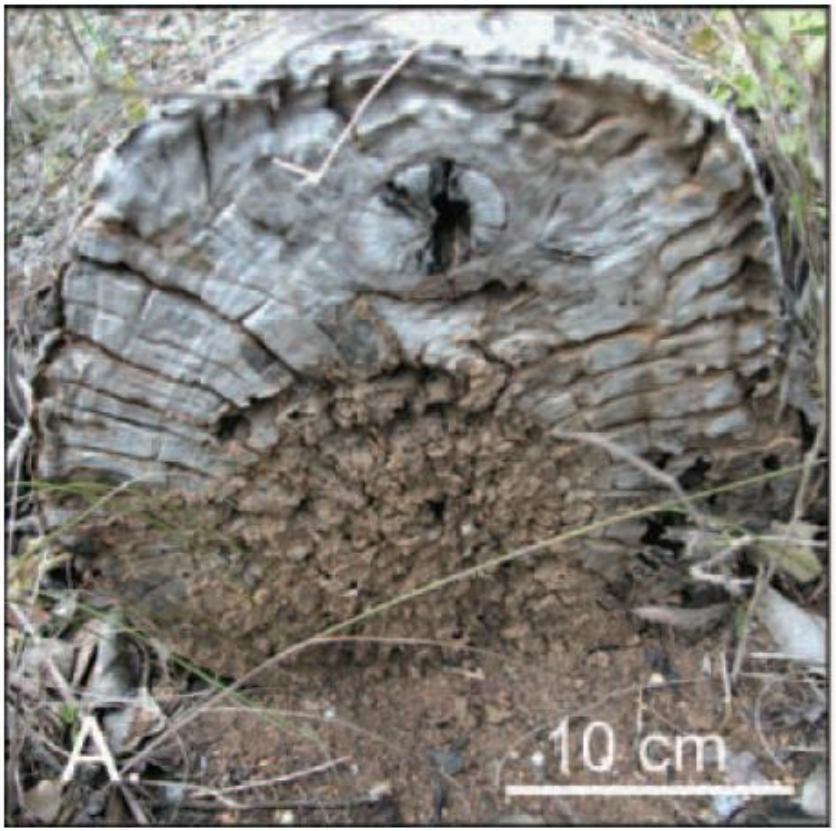
residues from lignin degradation are precursors for humus synthesis

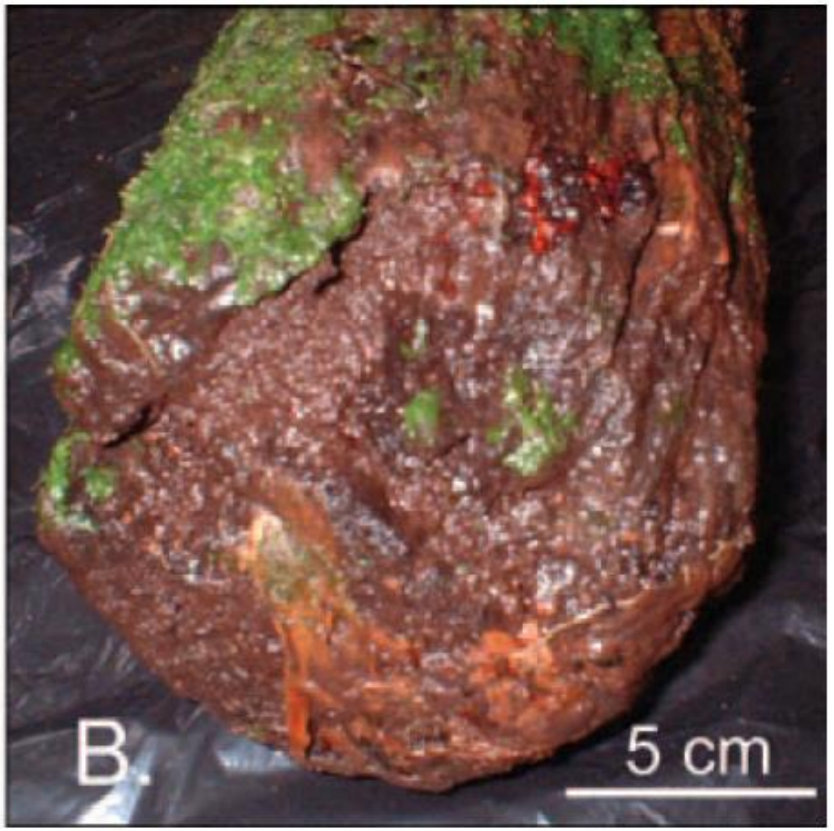
Deadwood

Measurable effects on chemical properties of the underlying soil

Translocation of dissolved organic matter (DOM)

Translocation of organic matter from woody litter to soil can occur via soil fauna as well





Cyrilla racemiflora in (a) tropical dry and (b) wet forests after 13 yr.
Notice the absence of bark, the presence of termite galleries and cracks, and how decay is faster near the ground in the dry forest (a). In contrast, observe mosses, water saturation, and no animal galleries in logs in the wet forest (b) (from Torres and González, 2005).

What is the effect of decaying logs on the physical, chemical and biotic characteristics of the soil underneath?

S. macrophylla (mahogany)

D. excelsa (tabonuco)

along the decomposition process

Hurricane Georges 1998 (6 yrs)

Hurricane Hugo (1989) (15 yrs)

Wood properties of *D. excelsa* and *S. macrophylla*

	Dacryodes excelsa Vahl	*Swietenia macrophylla* King
Family	Burseracea	Meliaceae
Common name	Tabonuco, gommier or candlewood[c]	Bigleaf Mahogany, caoba or caoba hondureña[c]
Distribution	Native to the West Indies[c]	Yucatan peninsula (23°N) to Brasil (18°S)[c]
Durability	Very susceptible[d,e]	Moderately resistant[d,e]
Lignin (%)	32.8[f]	45.8[f]
Wood density (g/cm^3)[a]	0.52–0.61[d,e,g,h]	0.4–0.68[d,g,i,j]
Hardness (lb)[b]	690–840[c,d,f]	740–1,160[d,j,k,l]

Ranges correspond to the maximum and minimum values reported in the literature

(Zalamea et al. 2007).

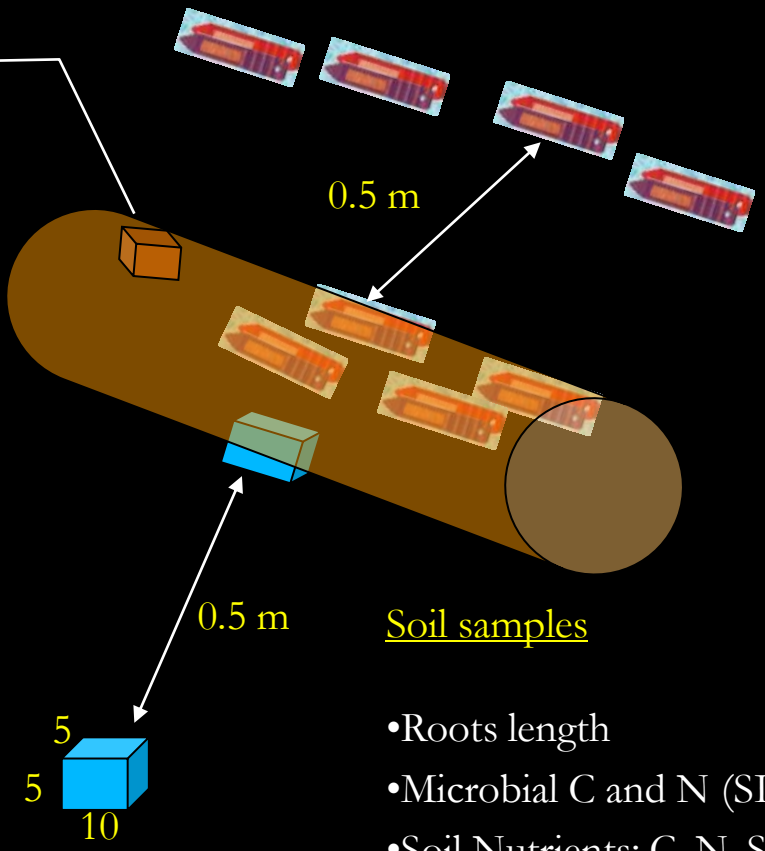
Soil Biota, Nutrients, and Organic Matter Dynamics Under Decomposing Wood, Sampling design

Wood samples

C Fractions: Lignin, Tannins, WSC, ASC, WSPS, ASPS

Nutrients: C, N, S, Ash (%); P, Al, Fe, Ca, Mg, Mn, Na, K (mg/g)

Wood density



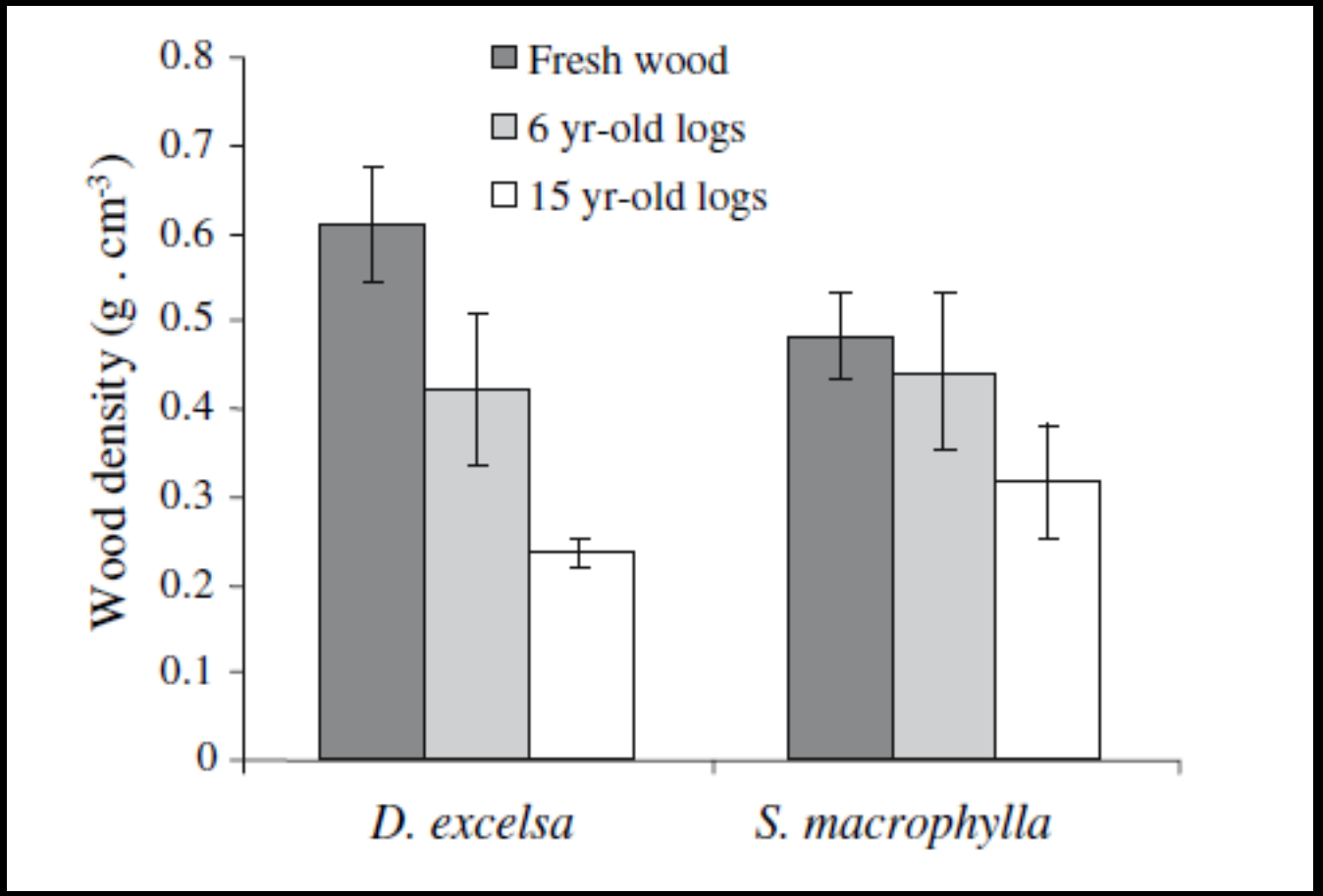
Available nutrients: Total N, NO_3, NH_4, P, Fe, Al, Ca, Mg, Mn, Na, K, and others

Soil samples

- Roots length
- Microbial C and N (SIR and CFE)
- Soil Nutrients: C, N, S, Ash (%); P, Al, Fe, Ca, Mg, Mn, Na, K (mg/g)

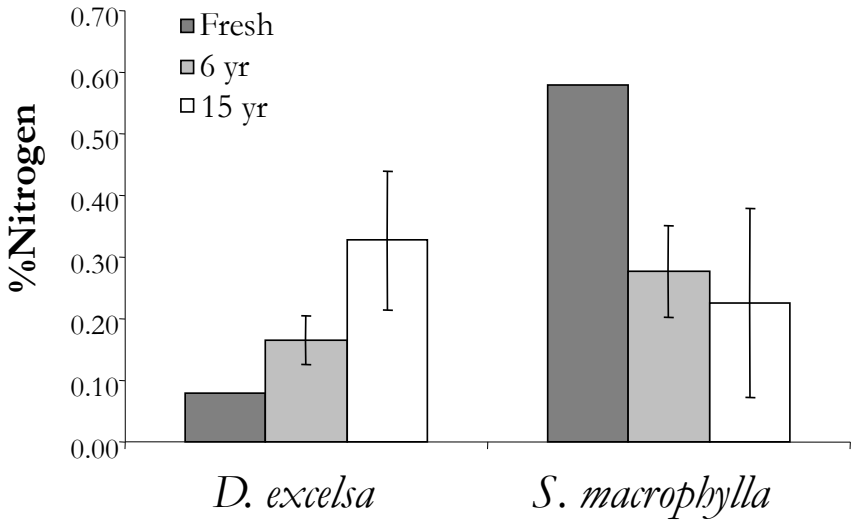
Environmental variables:
Air and Soil T°

Wood density for the two stages of decay and two species contrasted to fresh wood density



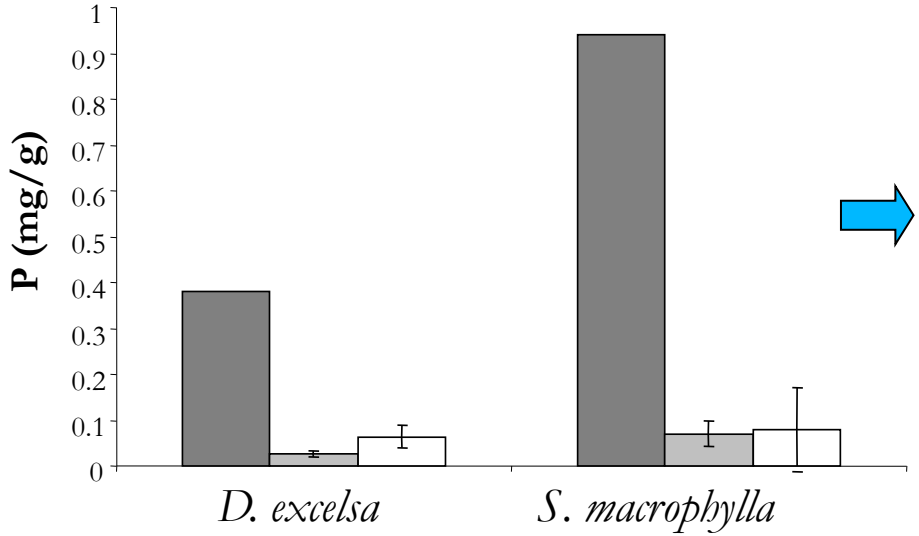
(Zalamea et al. 2007).

Nutrients in Wood



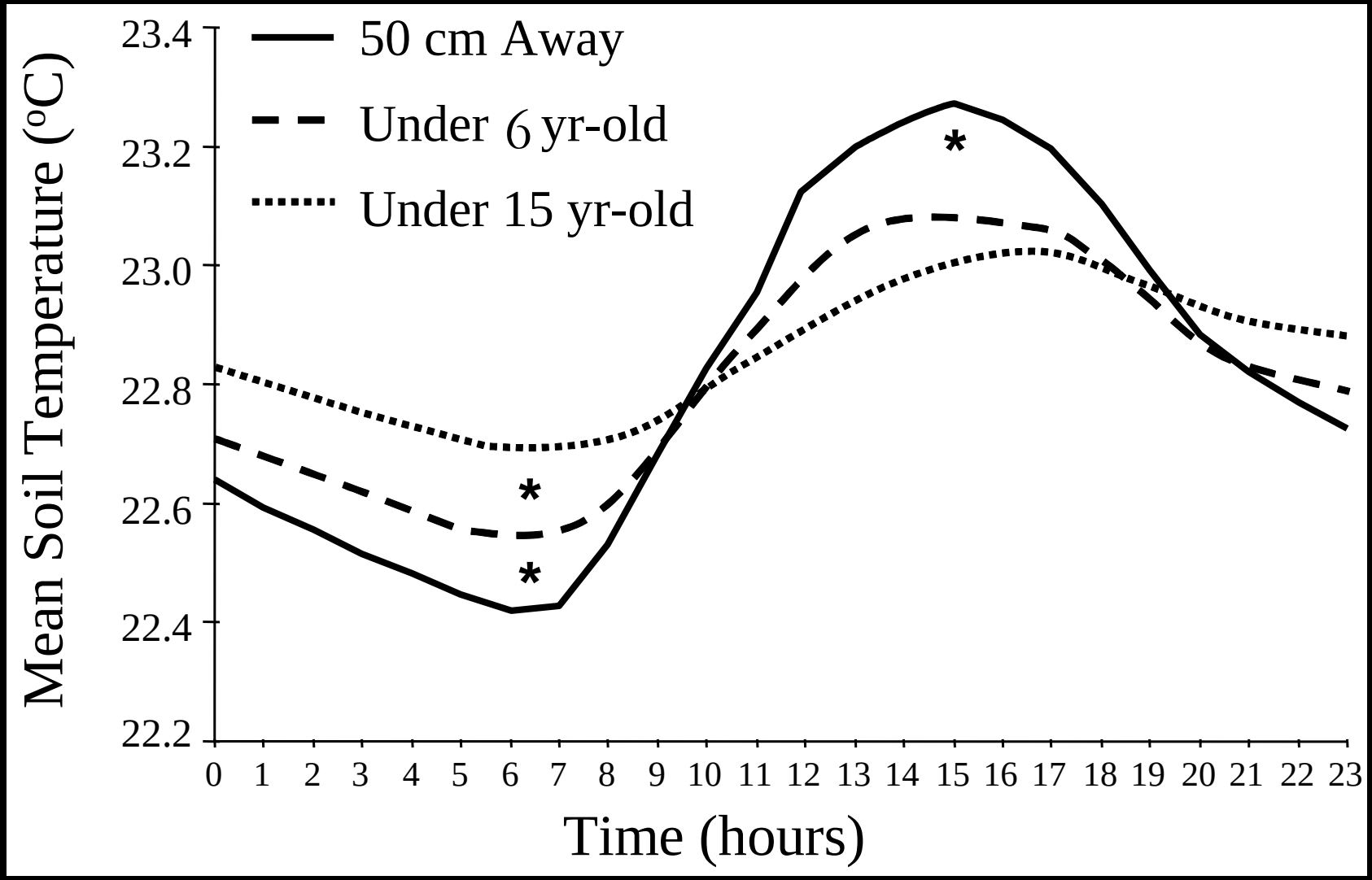
D.excelsa: N accumulation

S. macrophylla: N release, less decomposers biomass



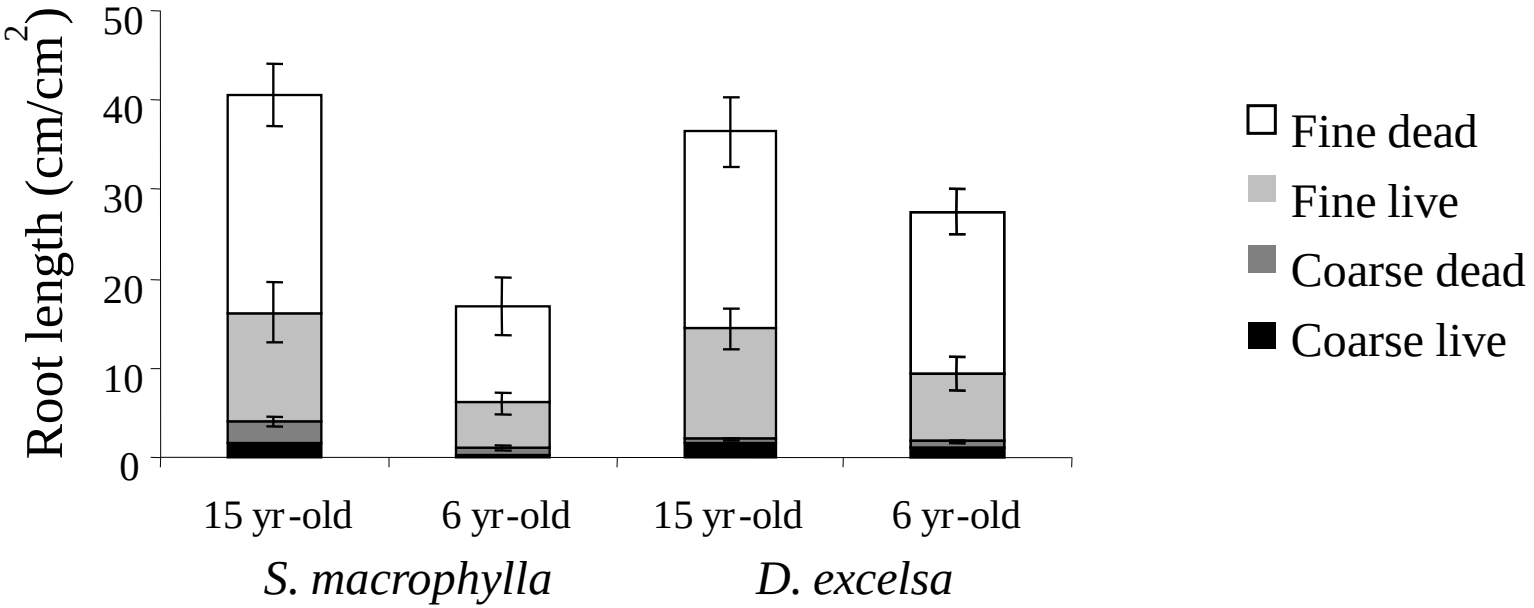
About 90% of P is lost at early stages

(Zalamea and González, unpub. ms).

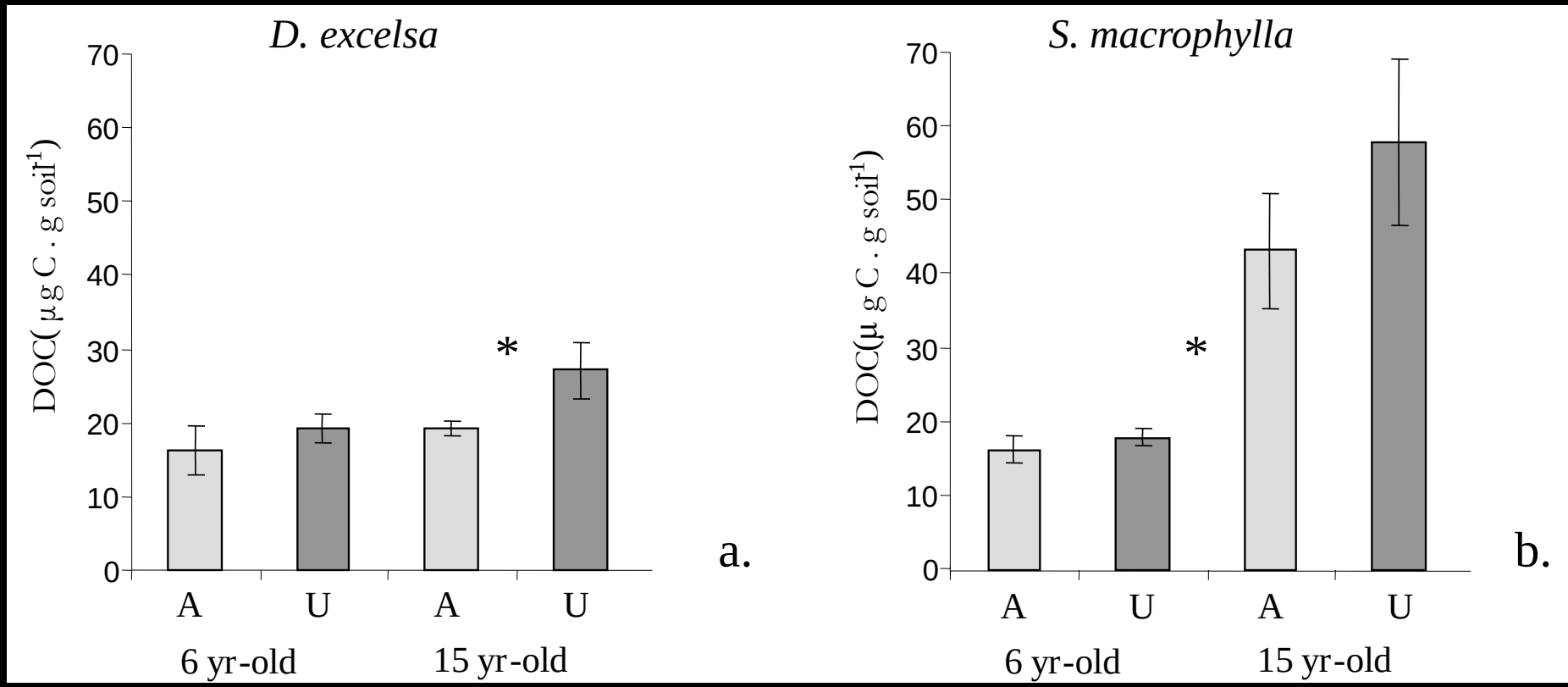


(Zalamea and González, unpub. ms).

Root length for coarse, fine, live and dead roots according to decay stage and species



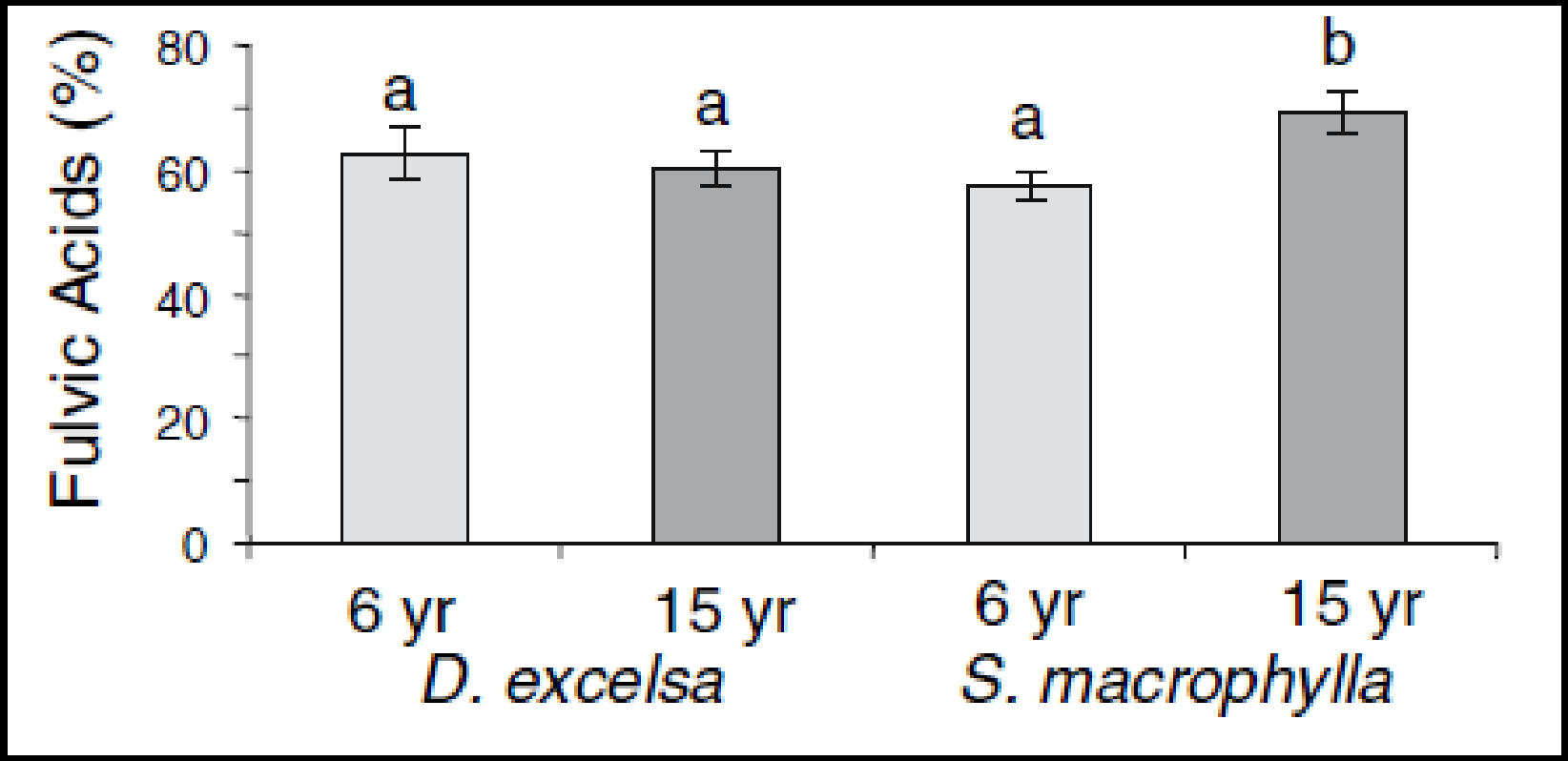
(Zalamea and González, unpub. ms).



Dissolved organic carbon (DOC) in soil under (U) and 50 cm away (A) from decaying logs. a) *D. excelsa*, b) *S. macrophylla*. * ($p < 0.05$).

(Zalamea et al. 2007).

Fulvic acids in the soil near (under and away positions averaged) decaying logs, according to species and decay stage



(Zalamea et al. 2007).

Conclusion

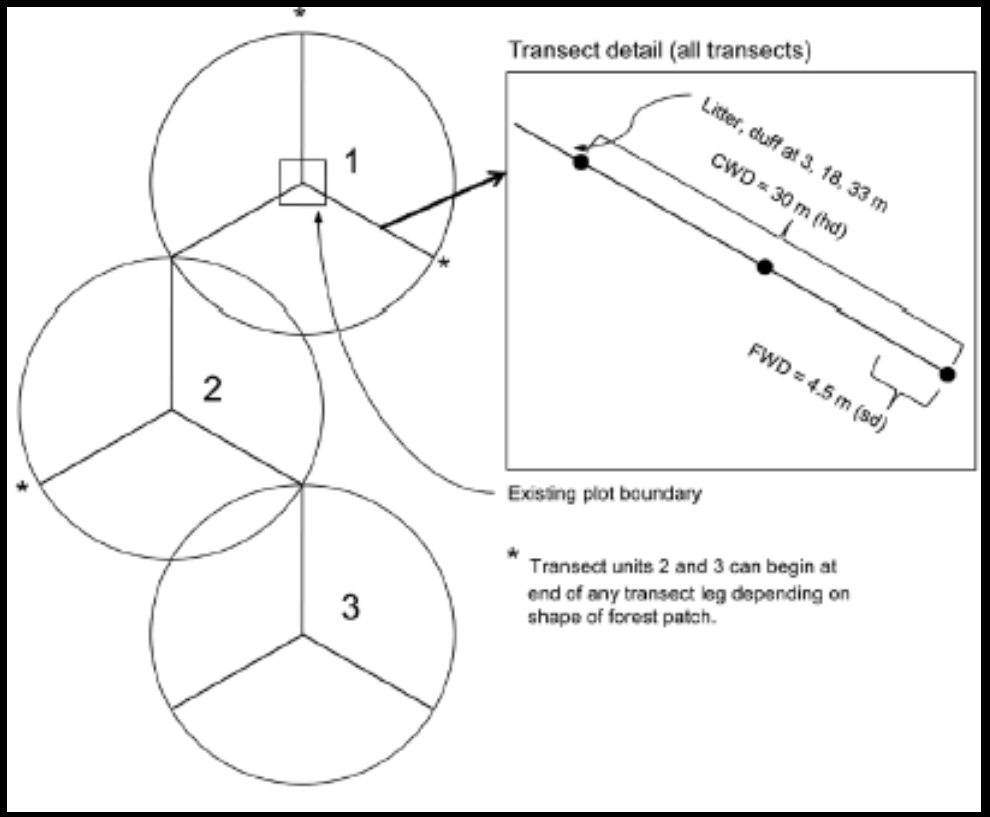
Decaying wood, through its effect on soil organic matter and nutrient dynamics, can contribute to the spatial heterogeneity of soil properties, and participate in processes of soil formation and nutrient cycling – in this tropical wet forest.

Average elevation (n = 3), annual precipitation (P), and temperature (T) within each forest type.

Forest type	Elevation (m)	P (mm/yr)	T (ºC)	
Mangrove	0	1565	25.7	
Dry	6	1451	26.4	Δ P ~ 1300 mm, Δ T ~ 4 ºC
Pterocarpus	12	1811	25.2	
Moist Lowland	36	1825	25.3	
Tabonuco	291	3537	24.5	
Colorado	769	4191	22.2	
Sierra palm	856	4167	20.7	Δ P ~ 3300 mm, Δ T ~ 5.2 ºC
Elfin (cloud)	957	4849	20.5	

(González et al, 2014)

Woody debris characterization along an elevation gradient in NE PuertoRico



Layout of the 3 transect units per plot with transect leg detail showing location of all measurements

Woody debris category	Diameter of wood (cm)	Fuel moisture time-lag (hour)
1 h FWD	< 0.60	1
10 h FWD	0.61–2.54	10
100 h FWD	2.55–7.59	100
1000 h CWD	> 7.60	1000+

Woody debris categories based on diameter of each woody category and fuel moisture time-lag values. Modified from Woodall and Monleon (2008).

(González and Luce 2014)

Mean mass of litter, duff, and all categories of WD (Mg / ha) in 8 forest types along an elevation gradient in NE Puerto Rico

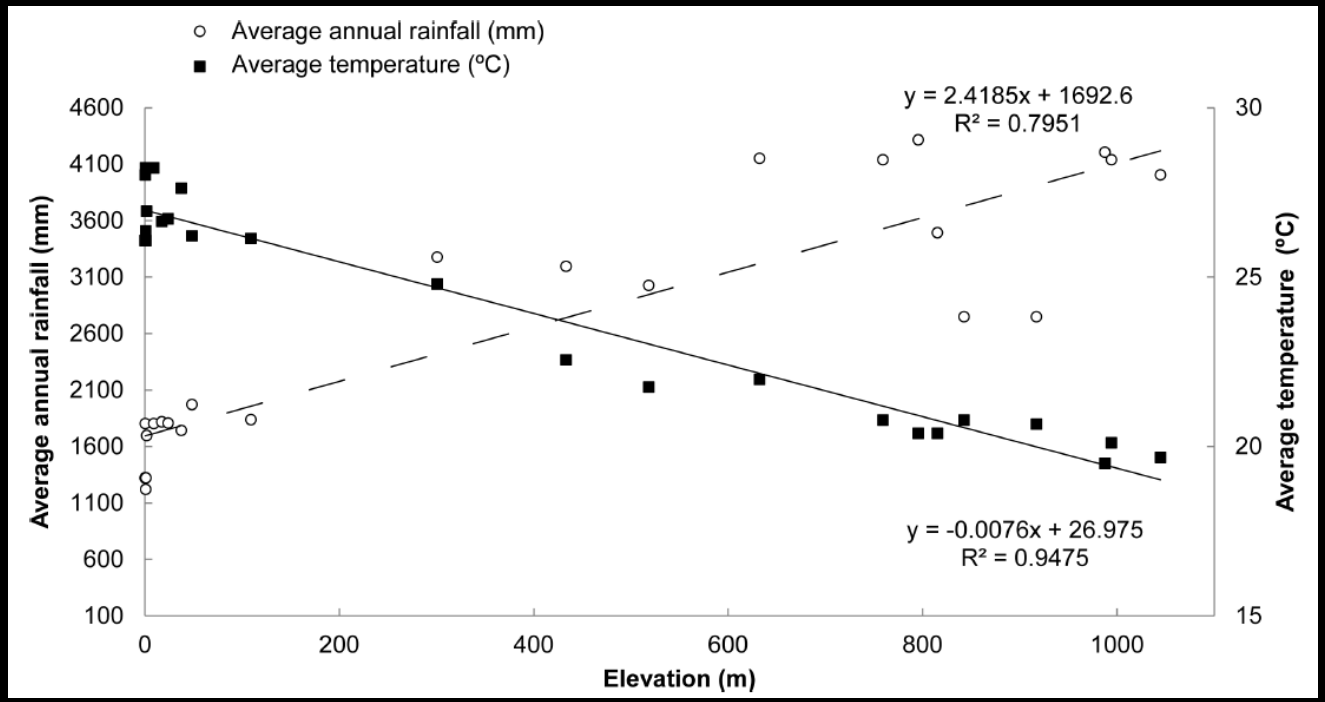
Category	R^2 (p value)	Mangrove	Dry	*Pterocarpus*	Moist	Tabonuco	Sierra palm	Palo Colorado	Elfin
Litter	0.22 (< 0.001)	0.12^{d}	0.91^{c}	1.12^{c}	1.29^{c}	2.59^{a}	1.90^{b}	1.44^{c}	1.19^{c}
Duff	0.10 (< 0.001)	0.00^{d}	0.68^{cb}	0.44^{c}	1.03^{a}	0.47^{c}	0.31^{c}	0.88^{ab}	0.52^{c}
1 h FWD	0.38 (< 0.001)	0.20^{bc}	0.35^{ab}	0.44^{a}	0.28^{bc}	0.31^{ab}	0.13^{c}	0.27^{bc}	0.18^{bc}
10 h FWD	0.31 (< 0.001)	2.63^{bc}	2.56^{bc}	4.91^{a}	3.07^{bc}	2.42^{bc}	2.39^{bc}	3.86^{ab}	1.52c
100 h FWD	0.26 (< 0.01)	10.12^{ab}	4.49^{b}	13.57^{a}	12.71^{a}	6.00^{ab}	9.19^{ab}	11.27^{ab}	5.99^{ab}
FWD – total	0.29 (< 0.01)	12.95^{ab}	7.39^{b}	18.91^{a}	16.06^{ab}	8.73^{b}	11.70^{ab}	15.39^{ab}	7.68^{b}
1000 h CWD	0.27 (< 0.01)	10.28^{b}	5.81^{b}	16.06^{ab}	21.75^{ab}	25.96^{ab}	40.60^{ab}	55.53^{a}	7.99^{b}
WD – total	0.30 (0.001)	23.23^{b}	13.2^{b}	34.97^{ab}	37.81^{ab}	34.69^{ab}	52.31^{ab}	70.92^{a}	15.67^{b}
Grand total (DWM)	0.31 (0.001)	23.35^{ab}	14.79^{b}	36.53^{ab}	40.13^{ab}	37.75^{ab}	54.52^{ab}	73.24^{a}	17.38^{b}

Common letters within a category of debris represent significant differences among forest types.

(González and Luce 2014)

Correlations for the elevation, mean annual precipitation and mean annual temperature , and litter , forest floor, 1–100 h FWD, total FWD, and CWD (Mg / ha)

Variable	Litter	Forest floor	1 h FWD	10 h FWD	100 h FWD	Total FWD	CWD
Elevation (m)	**0.28**	**0.24**	**–0.34**	**–0.19**	–0.10	**–0.14**	**0.27**
MAP (mm)	**0.35**	**0.25**	**–0.32**	**–0.21**	–0.10	**–0.14**	**0.28**
MAT (°C)	**–0.33**	**–0.29**	**0.28**	**0.15**	0.07	0.10	**–0.30**



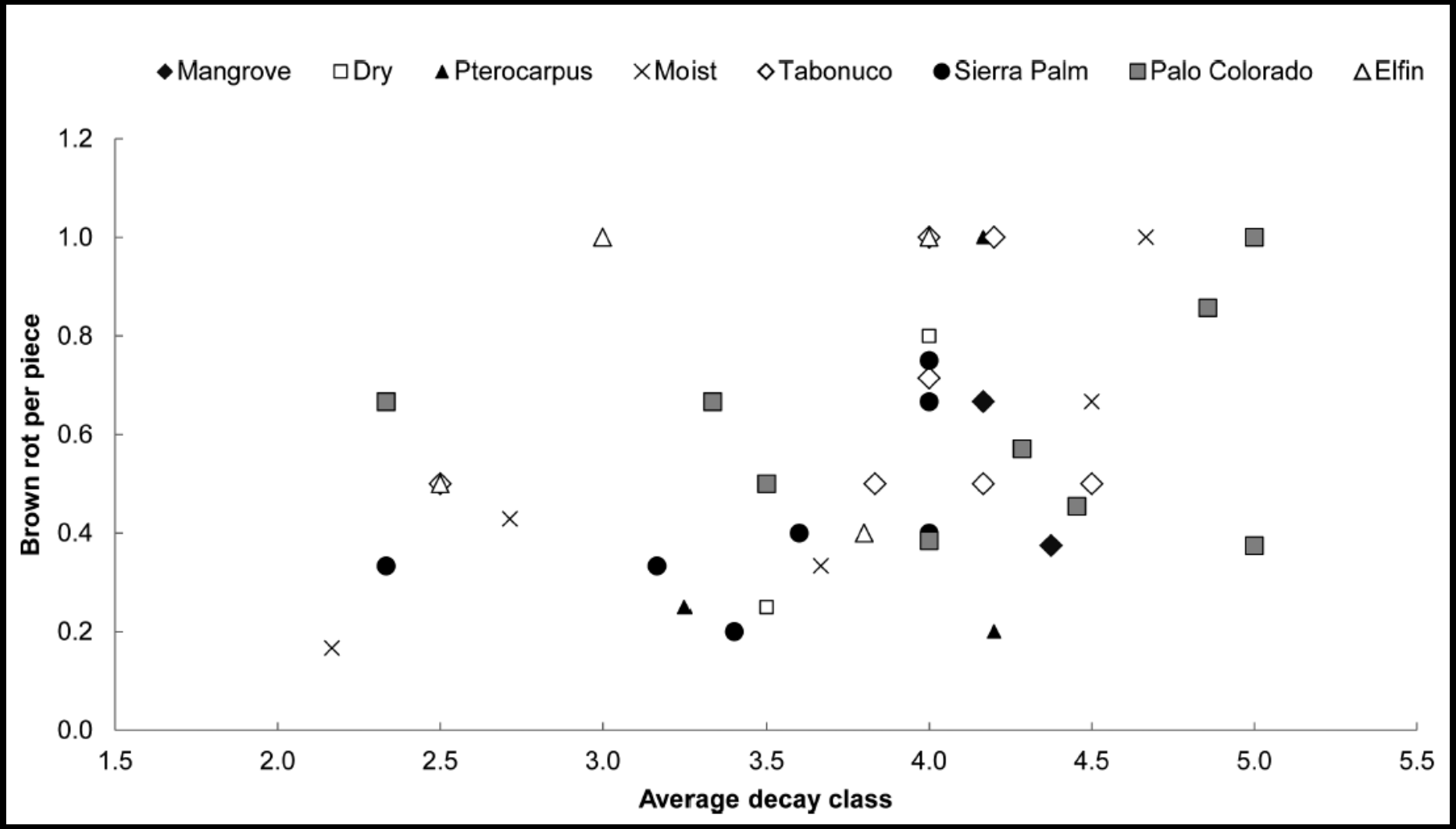
(González and Luce 2014)

Mean number of observed occurrences of brown rot, white rot, and termites (±SE) per piece of CWD in 8 forest types in NE Puerto Rico.

Forest types	Brown rot	White rot	Termites
Mangrove	0.17 (0.06) ^{b}	0.07 (0.04) ^{b}	0.17 (0.06) ^{bcd}
Pterocarpus	0.30 (0.06) ^{ab}	0.32 (0.06) ^{ab}	0.38 (0.07) ^{b}
Dry	0.37 (0.11) ^{ab}	0.21 (0.09) ^{b}	0.79 (0.09) ^{a}
Moist	0.50 (0.09) ^{ab}	0.27 (0.08) ^{ab}	0.33 (0.09) ^{bc}
Tabonuco	0.66 (0.09) ^{a}	0.14 (0.06) ^{b}	0.07 (0.05) ^{d}
Sierra palm	0.31 (0.07) ^{ab}	0.31 (0.07) ^{ab}	0.02 (0.02) ^{d}
Palo Colorado	0.55 (0.06) ^{a}	0.30 (0.06) ^{ab}	0.12 (0.04) ^{cd}
Elfin	0.35 (0.12) ^{ab}	0.53 (0.12) ^{a}	0.06 (0.06) ^{d}
F (p)	4.44 (< 0.001)	2.77 (0.008)	12.14 (< 0.001)

(González and Luce 2014)

Average decay class vs. number of occurrences of brown rot per CWD piece



(González and Luce 2014)

Conclusion

- Decomposer organisms are key determinants of wood decay in these forest types in NE Puerto Rico.

(González and Luce 2014)

Non-catastrophic annual inputs of coarse woody debris (>10 cm dia) for some tropical and temperate forests

Forest type and Location	Annual input of CWD (Mg/ha/yr)	Reference
Tropical-Subtropical		
Wet, Puerto Rico	1.97	Lodge 1996
Rain, Central Amazon	3.6	Chambers et al. 2000
Rain, Costa Rica	4.9	Clark et al. 2002
Temperate		
Coniferous, USA	0.3 – 4.5	Harmon et al. 1986
Deciduous, USA	0.3 – 14.5	Harmon et al. 1986

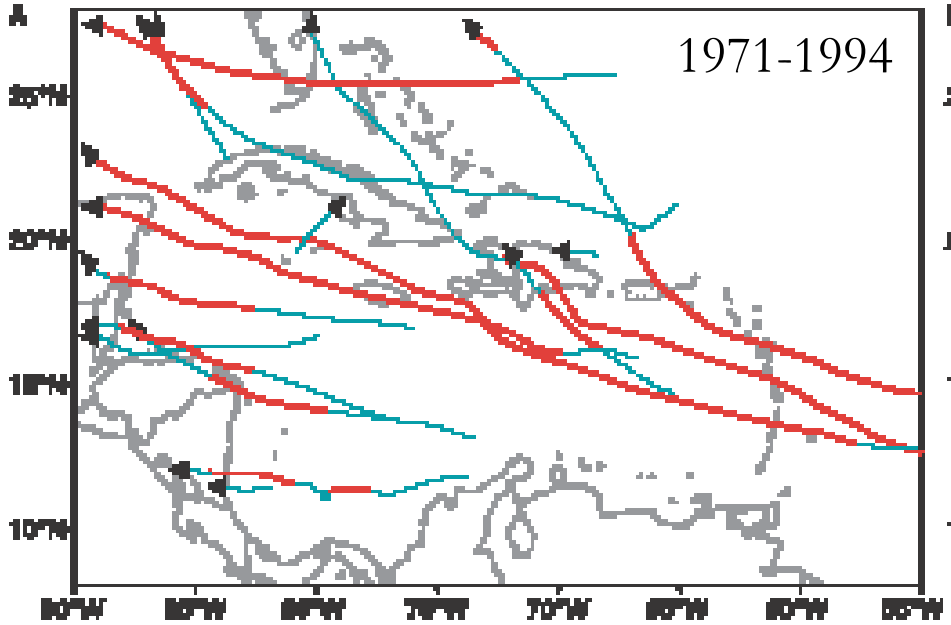
Hurricane Hugo generated 120 Mg/ha of CWD in NE PR (Scatena et al. 1993).

Almost 40-fold the mean background input rate for tropical forests

Caribbean hurricanes

Increased frequency and intensity (Emmanuel 1987, Goldenberg et al. 2001).

– high level of hurricane activity can persists for an additional ~10-40 yrs.



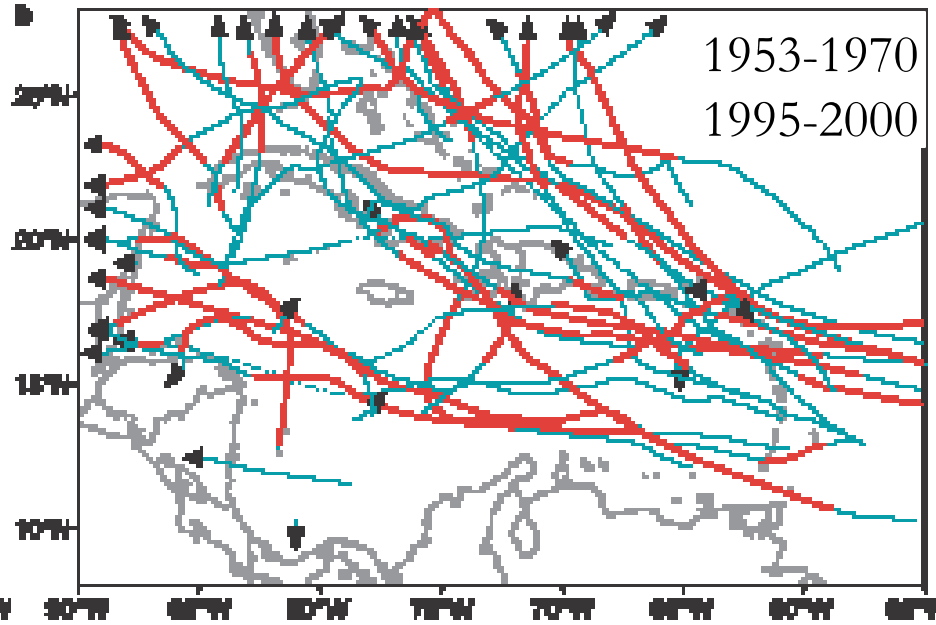


Fig. 4. Contrast of Caribbean hurricanes between colder (A) and warmer (B) values of the Atlantic multidecadal mode. The solid green (thin) and red (thick) lines indicate where the hurricanes were at nonmajor and major hurricanes intensities, respectively. Tropical storm intensity is indicated by dotted lines in cases where a hurricane weakened to tropical storm strength and then re-intensified to hurricane status. The years ar similar to (34) except that the first nine warmer years (1944–1952) ar not included to make the number of colder and warmer years equal. Th colder years (24 years) include 1971–1994. The warmer years (24 years include 1953–1970 and 1995–2000.

www.sciencemag.org SCIENCE VOL 293 20 JULY 2001

Goldenberg et al. 2001

Results of observations from hurricanes in PR

Hurricane Hugo, Bisley

6 months later

In the short-term, alteration of ecosystem processes.

Results of observations from hurricanes in PR

Canopy opening

Light levels, soil moisture, and temperature

Pulse of litterfall and woody debris

Quantity: After Hugo, total litter on the ground was ~1 kg / m^2 and 120 Mg/ha of CWD in NE PR.

Reposition: forest canopy into subcanopy and forest floor

(Lodge et al. 1991; Scatena et al. 1993 and 1996)

Luquillo LTER and Hurricane Simulation

Canopy Trimming Experiment (2003-2012)

- Separate effects of canopy opening and increased debris deposition
- Trimmed 576 trees, 30×30 m plots
- 3 blocks, 2 x 2 factorial experiment: (no trim+no debris, trim+debris, trim+no debris, no trim+debris)
- Measured forest responses (abiotic, biotic, biogeochemical processes)

FEM (Nov 2014), Special Issue, Tropical Forest Responses to Large-scale Experimental Hurricane Effects, Editors: Shiels and González

Wood Decomposition Experiment

Diameter classes

FWD 1

<1 cm diameter

20 cm length

FWD 2

1-2.5 cm diameter

30 cm length

FWD 3

2.5-7.5 cm diameter

40 cm length

Three categories of FWD and two species (*Dacryodes excelsa* and *Manilkara bidentata*) to determine decay rates in CTE plots.

Wood Decomposition Experiment

Percent mass remaining - data for 2 years, effect of DIF included

Dependent Variable:pmr

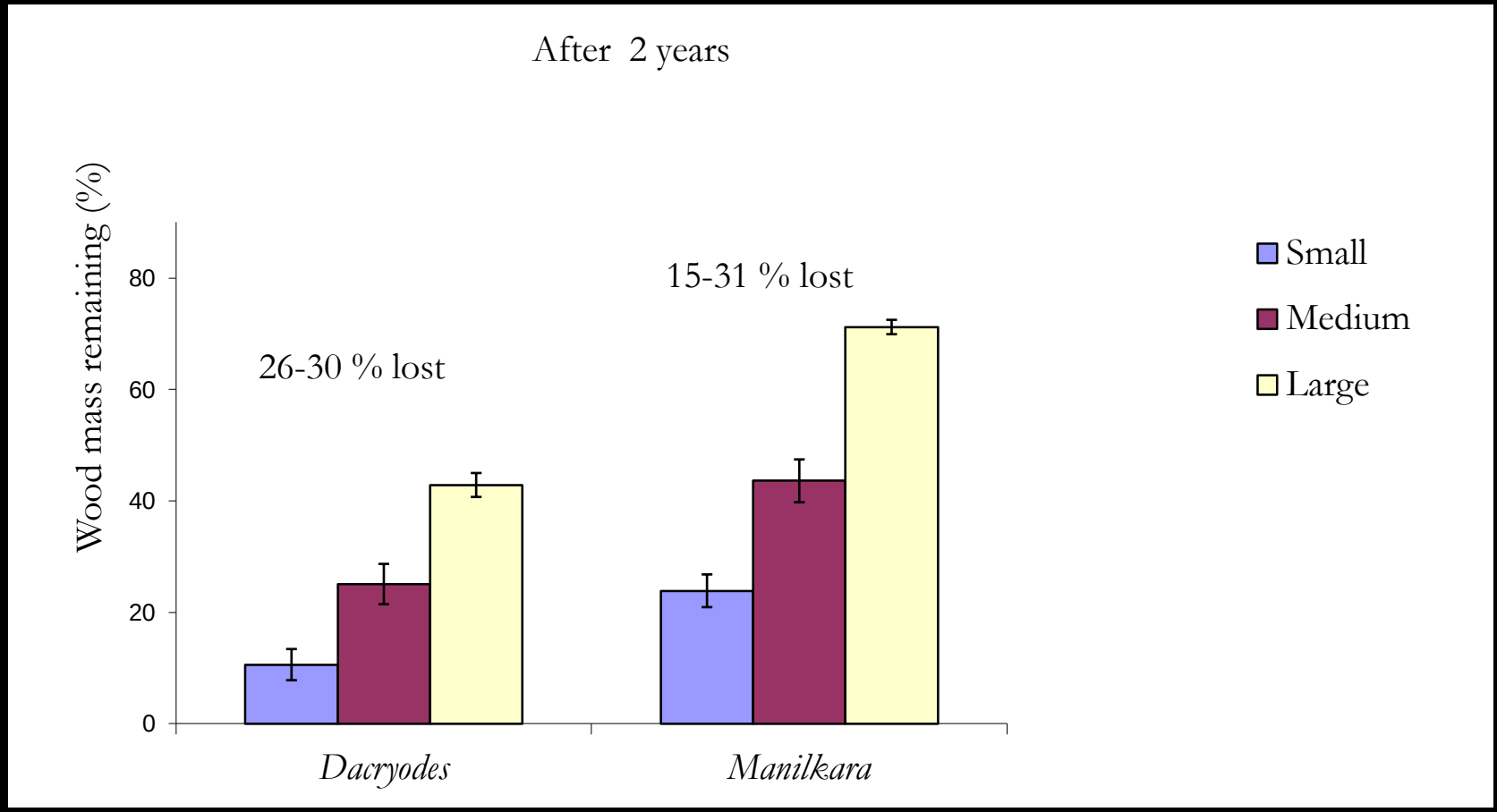
Source	Sig.	Noncent. Parameter	Observed Power[b]
Corrected Model	.000	5241.432	1.000
Intercept	.000	42710.818	1.000
Treat	.002	14.886	.914
Species	.000	392.391	1.000
Diameter	.000	968.164	1.000
dif	.000	3439.482	1.000
Treat * Species	.151	5.312	.464
Treat * Diameter	.194	8.667	.568
Treat * dif	.548	13.703	.620
Species * Diameter	.400	1.835	.209
Species * dif	.000	162.191	1.000
Diameter * dif	.000	175.633	1.000
Treat * Species * Diameter	.239	7.998	.528
Treat * Species * dif	.546	13.739	.621
Treat * Diameter * dif	.080	41.663	.977
Species * Diameter * dif	.002	28.032	.974
Treat * Species * Diameter * dif	.918	19.888	.667
Error			
Total			
Corrected Total			

a. R Squared = .822 (Adjusted R Squared = .799)

b. Computed using alpha = .05

(González et al. unpub. data)

Percent of mass remaining



(González et al. unpub. data)

Percent mass remaining – Treatment differences (all data)

pmr

Student-Newman-Keuls[a,,b,,c]

Treat	N	Subset 1	Subset 2
CC	321	67.0769	
CD	320	67.7454	
TR	319	69.1481	69.1481
TD	322		69.9737
Sig.		.068	.376

Means for groups in homogeneous subsets are displayed.
Based on observed means.
The error term is Mean Square(Error) = 139.006.

a. Uses Harmonic Mean Sample Size = 320.496.

b. The group sizes are unequal. The harmonic mean of the group sizes is used. Type I error levels are not guaranteed.

c. Alpha = .05.

(González et al. unpub. data)

Final comments, Implications

Logs have a significant effect upon soils underneath, this could help explain spatial heterogeneity in soil properties, such as nutrients availability.

Effects of decaying wood upon soil will depend also of changes in disturbance regime (dead wood inputs to soil):e.g. Increment in hurricanes frequency related with climate change.

Moisture condition is an important control over wood decomposition over broad climatic gradients; and that such relationship can be non linear

Particular group of organism (termites) can significantly alter the decay rates of wood more than what might be predicted based on climatic factors alone.

(González et al. 2008).